Patterns of geographic variation and evolution in polytypic butterflies

Paul C. Hammond

2435 E. Applegate, Philomath, Oregon 97370

Abstract. Patterns of geographic variation and evolution are examined in polytypic butterflies. It is concluded that genetic and evolutionary cohesion at the full species level is limited to monotypic organisms that are strongly vagile or migratory. Polytypic species with a fragmented population structure lack such cohesion, and each isolated population tends to function as an independent evolutionary unit. Taxonomic subspecies are usually the products of geographic isolation and differentiation, and represent separate phylogenetic lineages. Secondary intergradation between differentiated populations takes place in hybrid suture zones that often correlate with past geographic isolating barriers. Vicariance is a common phenomenon at the subspecific level in polytypic butterflies. Older populations survive as relicts in disjunct refugia, and are frequently surrounded by newer populations with more recently expanded distributions. There is no clear-cut distinction between a subspecies and a full species. A complete continuum is observed among differentiated populations with regard to reproductive isolating mechanisms and genetic or ecological compatibility. Speciation is strictly a secondary process that may or may not result from the primary process of macroevolution, the geographic differentiation of populations adapting to diverse environmental conditions. It is also suggested that macroevolution is usually characterized by peripatric cladogenesis and punctuated equilibria. As a consequence, extant insect populations have the dimension of time and ancestor-descendant relationships.

Introduction

One of the most controversial and perplexing questions in biology concerns the fundamental nature and evolutionary significance of geographic variation within species (see Wilson & Brown, 1953; Gillham, 1956; and Pimentel, 1959 for earlier reviews). This controversy still persists, and Arnold (1985) and Hammond (1986) have recently presented conflicting points of view. However, much has been learned about such variation in polytypic butterflies during the past thirty years, and it may be useful to review these questions in light of our current knowledge. In addition, basic theories of macroevolution have also advanced during this time.

Five different phenomena are included under the general subject of geographic variation. These include (1.) genetic gradients within cohesive populations called primary clines, (2.) differentiation between populations resulting from geographic isolation, (3.) secondary intergradation between previously isolated populations along hybrid suture zones, (4.)

vicariance and polytopic variation, and (5.) incipient speciation. In the present paper, I will consider lepidopteran examples of these phenomena and the taxonomic problems surrounding them. Current theories of macroevolution and punctuated equilibria are also of interest to this discussion.

Population Structure of Species

Much of the controversy regarding the nature of geographic variation is rooted in differing individual views of population structure within biological species. Mayr (1963) has presented one of the more comprehensive treatments of geographic variation in animal species. He believed that biological species are characterized by an internal genetic cohesion and homeostasis maintained by gene flow throughout all of the reproductively linked populations of the species. As a consequence, Mayr (1963, p. 348) concluded that geographic races or subspecies could not function as independent evolutionary units, and that geographic variation within species is of limited significance. He also suggested that speciation is the most basic process of evolutionary change. This process apparently takes place in complete geographic isolation by a so-called "genetic revolution," when the newly evolving population would be protected from the disrupting effects of external gene flow.

Many authors have embraced Mayr's point of view. For example, Rindge (1987) has recently expressed the opinion that geographic variation is of little or no scientific interest unless complete isolation exists between populations. Gould & Johnston (1972) have favorably reviewed multivariate studies that portray geographic variation as continuous with no spatial disjunctions, consisting of simple genetic perturbations within cohesive and panmictic gene pools. Futuyma (1979, p. 198) stated that "Infraspecific categories are simply constructs of our imagination, erected for the sake of convenience; we can recognize as few or as many races as we find convenient, for they have no independent biological reality". Likewise, Eldredge & Cracraft (1980, p. 16) have stated "We define species in such a way as to stress their internal cohesion, their identity as discrete, real entities, and their unique position as phylogenetic units. No taxon other than species serves as ancestors and descendants (*i.e.* as phylogenetic units) in evolution."

Most recently, some theorists have suggested that biological species may be viewed as phylogenetic "individuals" (Eldredge, 1989). Such entities experience birth (speciation), death (extinction), and selection (group selection) in a manner analogous to that of individual organisms. Of course, such theory depends upon the purported genetic cohesion of the biological species.

In sharp contrast, other authors have seriously questioned this concept of the cohesive species (Epling & Catlin, 1950). Ehrlich & Raven (1969) argued that many species are actually quite sedentary and display a highly fragmented population structure, with little or no gene flow

among the isolates. They also suggested that the real unit of evolution in such organisms is the locally isolated population, rather than the collective species. In the complete absence of gene flow, the only thing that local populations of a fragmented species really share with each other is a common phylogenetic ancestry, perhaps combined with similar stabilizing selection for the ancestral characteristics (Ehrlich & White, 1980).

The idea that geographic isolates constitute discrete evolutionary units and independent phylogenetic lineages is not new among lepidopterists. Rothschild & Jordan (1906, p. 429) regarded subspecies as incipient new species and basic units of evolutionary change, a view also shared by Fruhstorfer (H. Descimon, per. comm.) . Indeed, Karl Jordan was one of the first advocates of the modern subspecies concept (Mayr, 1976 p. 303). Grey & Moeck (1962) considered this with their discussion of geographic variation in *Speyeria* and other polytypic butterflies. Grey, Moeck, & Evans (1963) suggested that "the largest factor controlling population structure in butterflies is the residual inertia of genetic heritage, inferring that wing facies reflect earlier dispersal and isolation, relating only secondarily to present situations". Similar views were expressed by Bowden (1979) regarding variation in *Pieris*. Moreover, the philosophy behind the taxonomic classification of subspecies is based upon the existence and function of geographic isolates as independent evolutionary units and phylogenetic lineages.

Geographic variation within a cohesive and panmictic gene pool is of limited evolutionary and taxonomic significance as Mayr and other authors have rightly suggested. However, the genetically cohesive species is probably a relatively rare phenomenon in nature, at least among butterflies. Some species do appear to conform to the Mayrian model of cohesive population structure. These are usually migratory or highly vagile organisms, and they are generally monotypic with little or no recognizable geographic variation. Among North American butterflies, possible examples of cohesive species include *Danaus plexippus* (L.), *Vanessa cardui* (L.), *Colias eurytheme* Bdv., *Speyeria idalia* (Drury), and *S. edwardsi* (Reakirt). The last two species occupy the native tall-grass and short-grass prairies of the Great Plains, and their strong vagility appears to be an adaptation for quickly recolonizing large areas of habitat burned by periodic prairie fires. In sharp contrast, polytypic species in genera such as *Argynnis*, *Speyeria*, *Euphydryas*, *Melitaea*, *Limenitis*, *Papilio*, *Colias*, *Cercyonis*, *Erebia*, *Coenonympha*, *Lycaena*, *Callophrys*, and most polyommatine blues display a highly fragmented population structure that conforms to the Ehrlich-Raven model.

Differentiation of Populations

It is very important to distinguish between a primary genetic gradient within a cohesive population and differentiation between populations resulting from geographic isolation. These are entirely different phenom-

ena. Much discussion has appeared in the literature concerning this distinction, although many authors have felt that the two processes are difficult or impossible to distinguish in actual situations (*i.e.* Mayr, 1963 p. 380; Endler, 1977).

I tend to disagree with this view. Primary genetic gradients usually involve a simple polymorphism at a single locus or a few loci of a polygenic complex. It is not difficult to recognize such polymorphisms in actual populations. Good examples in Lepidoptera include the phenomenon of industrial melanism in moths such as *Biston betularia* L., the black and yellow morphs of *Papilio glaucus* L. and *P. bairdi* Edwards, and the alba female morph of *Colias* species. In such cases, the genetic basis of the polymorphism is usually quite simple (Robinson, 1971). However, most polymorphisms distributed along primary clines are probably not evident in the external morphology of the organism, but are internally "hidden" as with allozyme frequencies. The enzyme polymorphisms studied by Johnson (1976) in *Colias* populations are an example.

By contrast, the genetic differentiation that takes place between isolated populations commonly involves a major restructuring of the over-all genome, affecting many different loci on different chromosomes controlling completely unrelated characteristics. This involves not only changes in external morphology such as wing color pattern, but also changes in larval and pupal characters, ecological adaptations to different foodplants and temperature regimes, changes in allozyme systems and developmental rates, and changes in behavior. This is the so-called "genetic revolution" emphasized by Mayr (1963), characterized by a major reorganization of polygenic balances (Carson, 1982).

I believe that Mayr is correct in his view that geographic isolation is the primary factor behind major evolutionary divergence between populations. There are alternative theories for significant differentiation within a cohesive gene pool along a primary clinal gradient, including models for parapatric and sympatric speciation (Endler, 1977; White, 1978). However, such differentiation at dozens or even hundreds of independent loci on different chromosomes would appear to be very difficult to attain within a cohesive gene pool due to the disruption of gene flow and sexual recombination.

I also believe that most of the butterfly subspecies listed by Miller & Brown (1981) are in fact the products of geographic isolation. Arnold (1985) has been critical of "minor" subspecies that differ by only one or two characters of wing color pattern, implying that such variation may be a single allelic substitution along a primary clinal gradient. However, in most cases this view is not correct. "Minor" subspecies that only differ by a single morphological character are often found to differ by many other "hidden" biological characters as well. For example, McCorkle & Hammond (1988) found a number of biological differences between similar subspecies of *Speyeria zerene* (Bdv.). A particularly good example of "minor" subspecies are the tiger swallowtails of eastern North America,

Papilio glaucus glaucus, *P. g. canadensis* Roths. & Jordan, and *P. g. australis* Maynard. These three races are difficult to consistently distinguish on a morphological basis, but exhibit major biological differences in foodplant adaptations and pupal diapause characteristics (Scriber, 1986; Rockey, Hainze, & Scriber, 1987). Thus, even "minor" subspecies have evolutionary (adaptive) significance.

Microgeographic variation within a taxonomic subspecies is also of interest. For highly sedentary organisms, the subspecies has no more genetic or evolutionary cohesion than the full species. Indeed, many subspecies are fragmented into locally isolated populations that exhibit evidence of independent differentiation, and such populations only share a common phylogenetic ancestry. In western North America, each mountain range may have an endemic microrace, and individual mountains within a range may have local colonies or demes that are partially or completely isolated from other colonies. The evolutionary divergence within a complex polytypic species often shows a hierarchical arrangement consisting of local demes, microraces, subspecies,.and major subspecies groups.

For example, *Speyeria callippe elaine* dos Passos & Grey is a distinctive subspecies belonging to the *callippe* subspecies group along the West Coast. However, *S. c. elaine* is not homogeneous in western Oregon, and consists of five differentiated microraces distributed in (1.) high elevations of the Siskiyou Mountains, (2.) low elevations of the Siskiyous, (3.) low elevations north of the Siskiyous, (4.) high elevations in the Cascade Range, and (5.) low elevations in the Willamette Valley. Moreover, the microraces are comprised of local colonies that may be separated by five to ten miles. Such demes often exhibit minor differentiation, particularly if habitat conditions vary in different areas. In sedentary organisms, the local deme is probably the basic evolutionary unit, rather than the microrace, subspecies, or full species. In more vagile organisms such as *Speyeria coronis* (Behr), the taxonomic subspecies probably has some evolutionary cohesion.

Hybrid Suture Zones

If most taxonomic subspecies of polytypic butterflies are the result of evolutionary divergence during geographic isolation, clinal intergradation among such races is the result of secondary contact along hybrid suture zones. The characteristics of suture zones have received considerable attention in the literature (Mayr, 1963; Remington, 1968), and include three types of secondary intergradation. Many subspecies join together along an abrupt step-cline. This phenomenon may result from considerable genetic incompatibility between the subspecies or reduced ecological fitness of hybrid individuals. Indeed, Barton & Hewitt (1983) suggest that hybrid zones may serve as strong barriers to gene flow if multiple loci and characters are simultaneously involved in the geographic divergence. Conversely, the suture zone between many other

subspecies forms a long, gradual cline, indicating good genetic compatibility and ecological fitness of hybrids.

In the third type of intergradation, hybrid individuals exhibit superior ecological fitness over both of the parental genotypes, resulting in a fully developed reticulate fusion between previously differentiated subspecies. In such populations, the original parental phenotypes only appear as rare recombinants, and most individuals are of the intermediate hybrid phenotype. This last type of intergradation may be an uncommon occurrence in nature, however. Of the some 110 subspecies within the genus *Speyeria*, I have identified only six that appear to be of reticulate origin.

One example are the highly variable populations of *Speyeria mormonia* (Bdv.) in the northern Rocky Mountain and Canadian prairie regions. These may have originated from a hybrid fusion between S. *mormonia eurynome* (Edwards) of the southern Rocky Mountains and S. *m. artonis* (Edwards) of the Great Basin. Likewise, the Utah populations of *S. atlantis chitone* (Edwards) (=*wasatchia* dos Passos & Grey) are highly variable and intermediate between S. *a. nikias* (Ehrmann) of the southern Rocky Mountains and S. *a. tetonia* dos Passos & Grey of the northern Rocky Mountains.

It is useful to examine the intergradation between subspecies in greater detail. In most cases, hybrid suture zones are located along some type of geographic isolating barrier that either exists today or once existed in the past. Indeed, the distributions of many subspecies of North American butterflies strongly correlate with the major biogeographic regions and suture zones identified by Remington (1968).

As an example, *Speyeria aphrodite* (Fabr.) occupies a continuous distribution over much of eastern North America, and there are no geographic barriers within this region at present. Nevertheless, three distinctive subspecies join together near the Great Lakes as shown in Figure 1. Moreover, the hybrid suture zones among these races are fairly abrupt, suggesting some degree of incompatibility. The typical *S. a. aphrodite* is an East Coast subspecies with a westward extension into the Great Lakes region, *S. a. alcestis* (Edwards) occupies the native tall-grass prairies of the southern Great Plains, and *S. a. manitoba* (Chermock) occupies the northern Great Plains and Rocky Mountains.

Although these subspecies are not isolated at present, it is known that the Great Lakes region was buried under deep glacial ice fields during the Pleistocene some 15,000 years ago (Wells & Stewart, 1987). At that time, the three *S. aphrodite* subspecies were probably isolated in widely disjunct refugia along the East Coast, on the southern Great Plains, and in the northern Rocky Mountain region respectively. Following the retreat of the glaciers, the subspecies must have expanded their ranges to join together in the modern Great Lakes suture zone.

In western North America, high mountain ranges and lowland deserts have combined with the climatic fluctuations of the Pleistocene to form
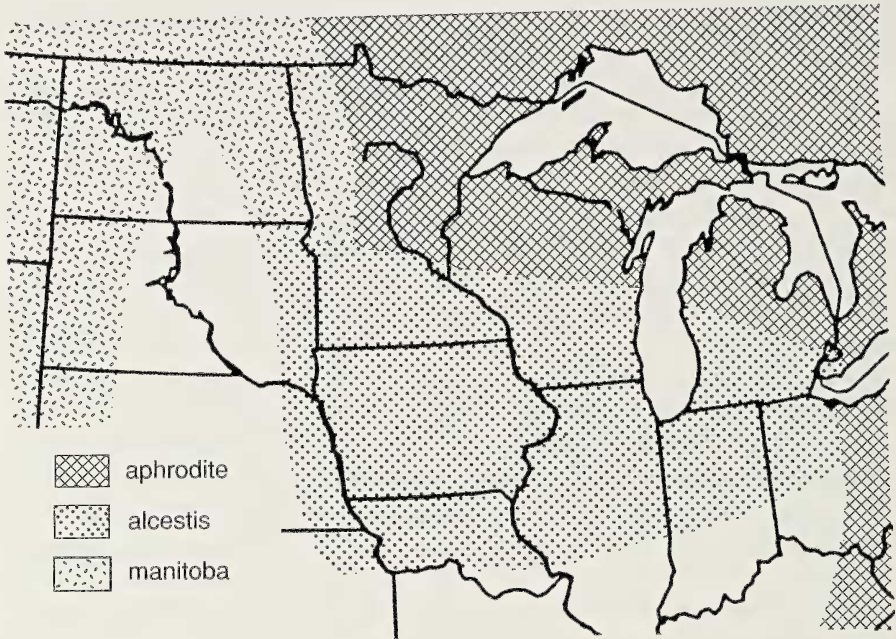
Fig. 1.   Distribution of *Speyeria aphrodite* subspecies in the Great Lakes region.

Fig. 2.   Distribution of *Speyeria callippe* subspecies in western North America.

strong isolating barriers at various times during the past two million years. Specifically, the mountains would serve as barriers during cold periods of glacial maxima, while lowland deserts would serve as barriers during warm interglacial periods. As a consequence, many butterfly genera exhibit extremely complex patterns of speciation and subspeciation within this region.

A good example is the geographic variation of *Speyeria callippe* (Bdv.) shown in Figure 2. The *callippe* group of subspecies are isolated along the West Coast from *S. c. semivirida* (McD.) and *S. c. nevadensis* (Edwards) by the high Cascade and Sierra Nevada ranges. Likewise, the high mountains along the Continental Divide have served to isolate two subspecies east of the Divide, including *S. c. meadi* (Edwards) along the Colorado Front Range and *S. c. calgariana* (McD.) on the northern Great Plains. In sharp contrast, lowland deserts have served to isolate *S. c. semivirida*, *S. c. nevadensis*, and *S. c. harmonia* dos Passos & Grey in the Great Basin and Intermountain regions. In fact, one of the major biogeographic suture zones discussed by Remington (1968) extends between these regions as shown by the *lorquini-weidemeyeri* suture zone in *Limenitis* and the *euryalus-gloveri* suture zone in *Hyalophora*. In addition to *S. callippe*, other species of *Speyeria* that exhibit an identical biogeographic distribution of subspecies across this region include *S. mormonia*, *S. zerene*, and *S. egleis* (Behr)

Polytopic Variation and Vicariance

One of the major criticisms directed towards the subspecies concept is the frequent spatial disjunction and discordant distribution of independent characters within a biological species (Gillham, 1956; Gould & Johnston, 1972; Arnold, 1985). This has been called "polytopic variation" (Mayr, 1963), and it is frequent in *Speyeria callippe* populations along the West Coast (Arnold, 1985). Such patterns may be explained as local and independent fluctuations in gene frequencies within a cohesive and panmictic gene pool. However, this can only be true for species with a cohesive population structure of the Mayrian model. For species with a fragmented population structure of the Ehrlich-Raven model, alternative explanations for polytopic variation must be considered. In addition, discordance among diagnostic taxonomic characters is frequently observed at the full species level (Hammond, 1986). Different species share different combinations of the same characters as subspecies. Of the 13 species of *Speyeria*, only four have consistent diagnostic characters that are not present in other species, and which do not vary geographically.

One explanation for discordance among different characters is convergent adaptation to similar environmental conditions by populations only distantly related to each other. A prime example is seen in pallid subspecies of *Speyeria atlantis* (Edwards). Most populations of this species live under cool, moist conditions, and display heavy, melanic basal suffusion on the dorsal wing surfaces combined with very dark disc

colors on the ventral hindwing. However, a number of *S. atlantis* subspecies are found in areas with warm, dry conditions, and these exhibit very pale wing colors. Such taxa include *S. a. helena* dos Passos & Grey on the Canadian prairies, *S. a. ratonensis* Scott in northeastern New Mexico, *S. a. greyi* Moeck in the Ruby Mountains of Nevada, *S. a. elko* Austin in the Independence and North Humboldt Mountains of Nevada, and *S. a. irene* (Bdv.) in the Sierra Nevada of California. Not only are these five subspecies widely disjunct in distribution, but their pale wing colors are quite discordant with other characters of the wing pattern. One may reasonably conclude that these populations are not closely related, and have acquired similar pale colors through independent convergence.

A second explanation for polytopic variation is vicariance (Rosen, 1978; Erwin, 1981). In species with a fragmented population structure, isolated populations tend to function as independent evolutionary units and phylogenetic lineages. Ancient subspecies that once enjoyed wide distributions may now survive only as relicts in widely disjunct refugia, while newer subspecies may now surround the refugia of the older subspecies. In these situations, there are often sharp ecological differences between the subspecies, which allows the older populations to survive within their restricted refugia. In addition, hybrid suture zones between the subspecies are often abrupt step-clines resulting from some degree of incompatibility. Otherwise, the older populations would tend to experience genetic swamping from the newer populations.

The recognition of vicariance is dependent upon two important factors. First, one must consider a time dimension for populations or taxa, since vicariance suggests a distribution through time. This will be discussed later under processes of macroevolution. Second, convergent similarities must be distinguished from phylogenetic similarities, not only to recognize examples of convergence or vicariance, but to establish a natural taxonomic classification. This is not always easy. Problems with character interpretation are ultimately reflected in taxonomic difficulties with the group in question. In *Speyeria* evolution, wing markings appear to be highly conservative and reliable as diagnostic characters, while wing colors are less stable. However, the darkness of color (*i.e.* melanic basal suffusion) is extremely plastic, and subject to repeated convergence and reversal (homoplasy). This is seen with the phylogenetic interpretations of *S. callippe* (Fig. 3, Table 1).

There is much evidence that vicariance is a relatively common phenomenon among polytypic butterflies in such diverse genera as *Papilio*, *Colias*, *Euphydryas*, *Speyeria*, *Coenonympha*, *Lycaena*, *Callophrys*, and *Icaricia*. For example, *Speyeria atlantis atlantis* is widely distributed in the Appalachians and across Canada to Alaska, but it also occurs in widely disjunct refugia through the Rocky Mountains from southern British Columbia to northern New Mexico. These refugia are surrounded by more divergent and probably newer subspecies of *S. atlantis* (Ferris, 1983).
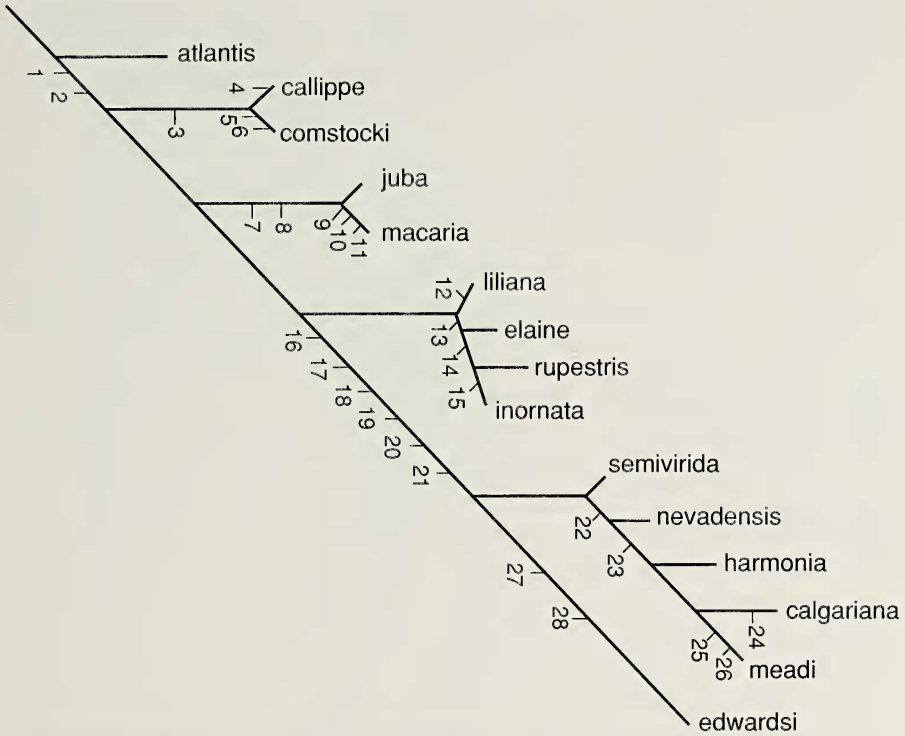
Fig. 3.   Cladistic analysis of *Speyeria callippe* subspecies.

Because most subspecies represent discrete evolutionary units, a phylogenetic analysis can be applied to them in a study of vicariance as discussed by Cracraft (1982). Thorpe (1984) used this approach with European snakes in order to distinguish between primary and secondary clines. As an example, a cladistic analysis of *Speyeria callippe* subspecies is shown in Figure 3, with individual character changes listed in Table 1. The species is probably derived from a West Coast isolate of the Appalachian-type *S. a. atlantis*. Indeed, the Oregon *S. c. elaine* is still remarkably similar to *S. a. atlantis*, while the California *S. c. callippe* and *S. c. juba* (Bdv.) are slightly more divergent from the putative ancestral type. One daughter species is apparently derived from *S. callippe*. *Speyeria edwardsi* probably evolved from a population of *S. c. semivirida* that became isolated on the northern Great Plains east of the Continental Divide in the same manner as *S. c. calgariana*, but at a much earlier time. In other words, *S. edwardsi* is likely a Pliocene or early Pleistocene isolate, while *S. c. calgariana* is probably an isolate of the late Pleistocene.

However, the oldest subspecies and the most complex geographic variation are found with the *callippe* group distributed along the West Coast in Oregon and California (Fig. 4). In phylogeny, this group divides
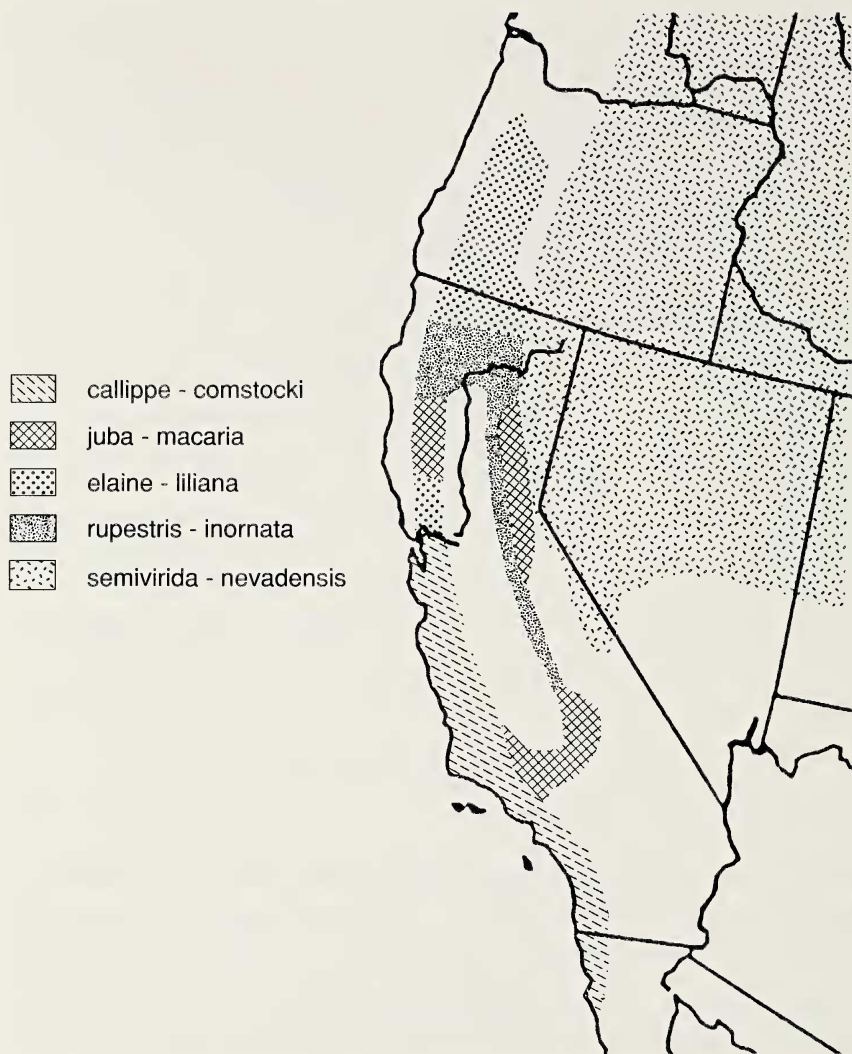
Fig. 4.   Distribution of *Speyeria callippe* subspecies along the West Coast.

Legend:
- callippe - comstocki
- juba - macaria
- elaine - liliana
- rupestris - inornata
- semivirida - nevadensis

into four distinctive pairs of subspecies, including (1.) *S. c. callippe* and
S. c. comstocki (Gunder), (2.) *S. c. juba* and *S. c. macaria* (Edwards), (3.)
S. c. elaine and *S. c. liliana* (Hy. Edwards), and (4.) *S. c. rupestris* (Behr)
and *S. c. inornata* (Edwards). But when the phylogenetic pairs are
compared with the distributions shown in Figure 4, wide disjunctions are
apparent.

The *callippe-comstocki* pair has a continuous distribution in the south-
ern California Coast Range. However, the *juba-macaria* pair is frag-
mented into three distinct isolates in the northern California Coast
Range, in the northern Sierra Nevada, and in the Tehachapi Mountains.
Likewise, the *liliana-elaine* pair is widely disjunct between Napa and

Lake Counties on the central California coast and western Oregon.
Finally, the *rupestris-inornata* pair is apparently derived from *S. c. elaine*, and occupies the Salmon-Trinity Mountains of northwestern California, extending southward in the western foothills of the Sierra Nevada to Tulare County.

Thus, the coastal *S. c. juba* population in Glenn, Tehama, and Mendocino Counties is inserted between the unrelated populations of *S. c. liliana* to the south and *S. c. rupestris* to the north. Likewise, the Sierran *S. c. juba* population is inserted between *S. c. inornata* to the west and *S. c. nevadensis* to the east, while *S. c. macaria* is connected to *S. c. comstocki* in the Coast Range and to *S. c. inornata* in the Sierras through the intermediate hybrid population called *S. c. laurina* (Wright) in the Greenhorn Mountains. Although hybridization is observed among all of these subspecies pairs, the suture zones are usually sharp step-clines that suggest some degree of incompatibility. Extensive reticulate fusion is only evident in the *laurina* population. In addition, sharp ecological differences are also present among the *inornata*, *juba*, and *nevadensis* populations of the northern Sierra Nevada.

The present distribution pattern is consistent with alternating contractions and expansions in diverse *S. callippe* populations during the climatic fluctuations of the Pleistocene. During cool glacial periods, the species may have disappeared from the mountains of northwestern California, only to re-expand into this region during warm interglacial periods. Originally only three subspecies were likely present along the West Coast if this interpretation is correct. These include the common ancestor of *callippe-comstocki* in the southern Coast Range, ancestral *liliana-elaine* in the northern Coast Range and western Oregon, and ancestral *juba-macaria* in the Sierra Nevada. An early glacial period could be responsible for the initial disjunction between *S. c. liliana* and *S. c. elaine*, followed by an expansion of the Sierran *S. c. juba* into the Coast Range during a subsequent interglacial period. Likewise, a later glacial period may have resulted in the disjunction of the coastal and Sierran *juba* populations. During a still later interglacial period, *S. c. rupestris* expanded and evolved from the Oregon *S. c. elaine* in the Salmon-Trinity Mountains, and eventually spread southward in the western foothills of the Sierra Nevada as *S. c. inornata*. Although this evolutionary hypothesis is complex, it would explain the complicated geographic variation present today along the West Coast.

Incipient Speciation

Patterns of geographic variation are also very complex in various degrees of incipient speciation, a process that is usually an extension of isolation and vicariant disjunction. Because polytypic species appear to lack genetic and evolutionary cohesion, the significance of speciation is largely of an ecological nature. Through the acquisition of reproductive isolation, closely related populations are able to co-exist in sympatry,

dividing available resources into ecological niches. Such resource parti-
tioning results in greater diversity and stability for the total ecosystem.
Thus, *Speyeria edwardsi* and *S. callippe* are widely sympatric on the
northern Great Plains.

The term "semispecies" has been applied to geographic segregates that
exhibit a trend towards speciation (reproductive isolation), and polytypic
species that consist of semispecies have been called "superspecies"
(Mayr, 1963). In nature, there is often no clear-cut distinction between a
geographic subspecies and a fully distinct biological species as Ehrlich
(1961), Lorkovic (1962), Ehrlich & Murphy (1983), and Clarke & Larsen
(1986) have discussed with butterflies. This fact supports Mayr's belief
that most speciation is an allopatric process.

Because speciation is an important result of the geographic differentia-
tion of populations, it is useful to examine this process in greater detail,
and butterflies provide many examples at four different stages of diver-
gence. These include (1.) divergent subspecies with no reproductive
isolation, (2.) divergent subspecies with reproductive isolation in re-
stricted local areas, (3.) allopatric populations that are intermediate in
morphology between fully distinct sympatric species, and (4.) fully
distinct sympatric species that exhibit reticulate hybrid fusion in re-
stricted local areas.

There are many examples of highly. divergent subspecies that lack
reproductive isolating mechanisms, as with the *Speyeria callippe* sub-
species along the West Coast. Most of these populations have been
regarded as distinct taxonomic species in the past (dos Passos & Grey,
1947). Other examples in North America include the *Limenitis arthemis*
complex (Platt, 1983), the *Papilio glaucus-rutulus* complex (Brower,
1959), and the *Papilio machaon* complex. In the latter group, the taxa
asterius Cramer, *zelicaon* Lucas, and *hudsonianus* Clark have always
been regarded as distinct species, and they are quite divergent in both
wing color pattern and allozyme patterns (Sperling, 1987). Nevertheless,
these taxa lack reproductive isolation, and they form extensive hybrid
swarms within their suture zones. Moreover, there is evidence that this
secondary intergradation is not a recent or temporary phenomenon, but
has persisted for hundreds or even thousands of years since the last
glaciation (Sperling, 1987). Similar stability of hybrid swarms has also
been detected in *Hyalophora* moths (Collins, 1984).

Other highly divergent subspecies intergrade in most areas of their
ranges, but exhibit reproductive isolation in a few local areas of overlap-
ping sympatry. For example, *Speyeria atlantis* subspecies exhibit exten-
sive intergradation throughout most of the species' range. Indeed,
populations in the Rocky Mountains of Montana are joined together in a
massive, three-way hybrid swarm between the northern *S. a. beani*
(Barnes & Benj.), the central *S. a. tetonia*, and *S. a. helena* of the
Canadian prairies.

However, in some local areas, *S. atlantis* subspecies co-exist together

in sympatry with strong reproductive isolation, for example in the Riding Mountains of Manitoba (Moeck, 1957) and the Black Hills of South Dakota (Grey, Moeck & Evans, 1963). Likewise, Ferris (1983) and Scott (1988) have recently looked at the partial segregation between *S. a. atlantis* (=*electa* Edwards) and *S. a. hesperis* (Edwards) along the Colorado Front Range. My own field observations in western Colorado indicate that *S. a. atlantis* and *S. a. nikias* are widely sympatric with strong reproductive isolation south of the Gunnison River. However, the *S. atlantis* populations north of this river are an intermediate mixture between typical *atlantis* and *nikias*, apparently resulting from a hybrid fusion between these races.

A slightly different version of incipient speciation involves sympatric populations with allochronic flight periods. Mattoni (1989) has provided several examples of sympatric allochrony in the *Euphilotes battoides* complex. David V. McCorkle and I have observed a good example in *Euphydryas editha* (Bdv.). Two subspecies of similar phenotype are distributed along the western slopes of the Cascade and Sierra Nevada ranges. The Cascadian race is named *E. e. colonia* (Wright), the larvae feed on *Castilleja* spp. , and the adults fly in June and July. By contrast, the Sierran race is named *E. e. rubicunda* (Hy. Edwards), the larvae feed on *Collinsia* spp., and the adults fly in April and May (Ehrlich & Murphy, 1981). Very similar populations are also found in the Siskiyou Mountains of southwestern Oregon and adjacent California. These have been called "*baroni*" by Dornfeld (1980), although the true *E. e. baroni* (Edwards) is apparently restricted to the California coast in Mendocino County (Murphy, 1983).

In fact, the Siskiyou populations consist of two sympatric and allochronic units, although the adults are nearly identical in phenotype. A *rubicunda*-like population lives in dry, rocky habitats, and the adults fly from late March through May with oviposition on *Collinsia*. A sympatric *colonia*-like population lives in *Darlingtonia* bogs and riparian areas, and the adults fly in June and July with oviposition on *Castilleja*. Although the adults occur in the same areas with a mixture of bogs and rocky outcrops, the different flight periods must preclude most gene exchange between these populations. In terms of reproductive isolation, they are functioning as distinct species.

The third situation arises from the geographic fragmentation of populations that precedes speciation. These are allopatric populations that are intermediate in morphology between distinct sympatric species, and are difficult to classify at the species level. For example, *Speyeria zerene* and *S. coronis* are sympatric throughout most of the western United States. Although closely related, they clearly function as distinct species. However, two allopatric populations are intermediate between these species, including *carolae* (dos Passos & Grey) in the Spring Mountains of Clark County, Nevada and *semiramis* (Edwards) in southern California. The *carolae* population was originally described as a *S. coronis*

subspecies, but was later transferred to *S. zerene* by Grey & Moeck (1962). Likewise, the very similar *semiramis* exhibits reproductive linkage with other *S. coronis* populations, but it still retains many of the characteristics of *S. zerene*.

There are similar examples in other genera such as *Colias* and *Papilio*. *Colias pelidne* Bdv. & LeC. and *C. gigantea* Strecker are widely sympatric in the northern Rocky Mountains, and are fully distinct with different larval foodplants (Ferris, 1987). However, an allopatric population in the Rocky Mountains of Colorado is intermediate and apparently feeds on both foodplants. Ferris (1987) has chosen to deal with this difficult taxonomic problem by treating the Colorado population as a third distinct species, *C. scudderi* Reakirt. Likewise, *Papilio astyalus* Godart and *P. androgeus* Cramer are sympatric through much of tropical America. However, an allopatric population named *P. thersites* Fabr. is isolated on the island of Jamaica, and is intermediate in wing pattern between the continental species. Although treating allopatric populations as distinct species provides an easy solution to embarrassing taxonomic problems, it also obscures the intermediate transitions between sympatric species. Such transitions are quite common in nature, but their existence is not recognized by the Linnaean system of taxonomic nomenclature.

Finally, the fourth situation involves widely sympatric species that remain distinct in most regions, but exhibit hybridization and reticulate fusion in certain local areas. *Euphydryas chalcedona* (Dbl.) and *E. anicia* (Dbl.) are usually distinct species in most parts of their sympatric ranges (Ferris, 1988a), but reticulate fusion between them is evident in parts of Nevada and northeastern California (Scott, 1980). A similar situation exists between *Colias pelidne* and *C. interior* Scudder. Although these species appear to remain distinct in most parts of their ranges, apparent hybrid populations are found in Idaho (Ferris, 1988b). There is also evidence that local areas of hybridization and fusion occur in several other butterflies of the Pacific Northwest, including hybrid swarms between *Colias occidentalis* Scudder and *C. alexandra* Edwards, and between *Lycaeides melissa* (Edwards) and *L. idas* (L.) (unpublished data).

Processes of Macroevolution

The theory of macroevolution has changed considerably since Darwin, and even since formulation of the "modern synthesis". Stebbins & Ayala (1981) have suggested that macroevolution is an autonomous field of evolutionary study, because macroevolutionary patterns cannot be deduced from the microevolutionary principles of mutation, gene flow, random drift, and natural selection. Thus, the processes of macroevolution can only be examined by studying actual patterns of past divergence and adaptive radiation.

Various theories of macroevolution have been reviewed by Mayr (1963,

1976), Stanley (1979), Eldredge & Cracraft (1980), and Eldredge (1989). At first, it was thought that most evolution took place by phyletic gradualism within cohesive gene pools. This model suggested that established populations slowly change over long periods of time in response to gradually changing environmental conditions. However, the fossil record provided support for an entirely different pattern of macro-evolution; one characterized by short, explosive bursts of evolutionary change followed by long periods of relative stasis. Such evidence resulted in theories of saltation, quantum evolution, and punctuated equilibria (Gould & Eldredge, 1977).

Under the model of punctuated equilibria, macroevolution does not take place by phyletic change within established populations, but through the creation of entirely new populations (cladogenesis). Moreover, the process rarely involves a dichotomous splitting of a pre-existing ances-tral population into two daughter populations. Instead, macroevolution is usually associated with peripheral budding (peripatric cladogenesis) at the perimeter of the ancestral population's range where environmen-tal conditions are different (Mayr, 1976 p. 455; 1982). The ancestral population remains intact and unchanged within the original environ-ment, while the new daughter population actively invades and adapts to an entirely new environment (Eldredge & Cracraft, 1980 p. 125). Indeed, only a few generations of intense directional selection within a small founder population may be required to achieve significant adaptive shifts (Ford, 1945 pp. 268-270; Carson & Templeton, 1974; Dimock & Mattoni, 1986). Thus, peripatric cladogenesis combined with adaptive shifts to new environmental conditions are now thought to be the most important factors behind macroevolution.

However, Mayr and Eldredge still believe that cladogenesis is essen-tially synonymous with speciation due to the purported cohesion of the biological species (Eldredge, 1989). This view is rejected in the present paper for the reasons previously discussed. Instead, I would argue that the basic process of macroevolution is the geographic differentiation of populations, and not necessarily speciation. Likewise, if one wants to directly observe the process of macroevolution, they should examine patterns of geographic variation, and not patterns of speciation.

There are other far-reaching implications. It is frequently argued that populations or taxa do not have the dimension of time, because a population of today is never precisely identical to a population of yester-day. Thus, no living population can be directly ancestral to any other living population. While this argument is partly a matter of semantic definition, it is also a corollary of phyletic gradualism. However, if punctuated equilibria and peripatric cladogenesis are real phenomena, then populations do have dimensions of both time and space. Presently extant populations may be regarded as "ancient" or "recent" on the time scale, and may be regarded as "ancestral" or "descendant" in phylogeny.

In addition, ancestral forms of insects face a low probability of extinc-

tion as descendants evolve, in contrast to the extinction patterns of large
vertebrates seen in the fossil record. Insects are able to survive as relicts
in small, isolated refugia that could never support a viable population of
large vertebrates. At the full species level, reproductive isolation and
resource partitioning allow large numbers of related insect populations
to co-exist in sympatry, including both ancestral and descendant popu-
lations. For example, eight species of *Speyeria* are widely sympatric in
western North America. But the four species of the primate genus *Homo*
follow each other sequentially in the fossil record, and never co-existed
together for long periods of time (Rightmire, 1985). Although these
primates present the pattern of punctuated equilibria, paleontologists
cannot decide if *Homo* evolution has been phyletic or cladogenic (Eldredge,
1989 p. 75). There is no such doubt with extant butterfly taxa. It is only
through cladogenesis that related populations can exist simultaneously
in time.

The previous examples of *Speyeria atlantis* and *S. callippe* serve to
illustrate punctuated equilibria, peripatric cladogenesis and ancestor-
descendant relationships. In particular, the Appalachian-type S. *a.
atlantis* appears to represent a basal-stem ancestor within the genus
Speyeria, and is a prime example of punctuated equilibria. This subspe-
cies displays a classical vicariant pattern, with a continuous Appala-
chian population and three widely disjunct Rocky Mountain populations.
One extends from northern Idaho to southeastern British Columbia, a
second occurs in the Big Horn Mountains of Wyoming, and a third occurs
in Colorado. A fourth population in the Black Hills of South Dakota is
more derived, and appears to be closely related to *S. a. hollandi* (Chermock)
in the Riding Mountains of Manitoba. All of these populations are
surrounded by highly derived subspecies of *S. atlantis*.

There has certainly been no direct genetic contact among the Rocky
Mountain populations of *S. a. atlantis* for the past 12,000 years and
generations since the last glacial period, and possibly for much longer
considering the distributions of the surrounding subspecies. Genetic
contact between the Appalachian and Rocky Mountain populations has
clearly been broken for a very long time. Yet no major differentiation has
taken place among these populations. This long-term stasis is closely
correlated with the ecology of *S. a. atlantis*, since all disjunct isolates of
this subspecies still occupy a similar habitat consisting of cold, wet
spruce or birch forests. In sharp contrast, the surrounding subspecies
occupy warm, dry forests of pine, fir, and aspen, or even open grasslands
on the Canadian prairies.

The cladogram in Figure 3 depicts the distribution of derived charac-
ters among the taxa of the *Speyeria callippe* group. However, cladograms
do not give a time dimension to taxa, and simply arrange taxa in a
dichotomous branching pattern. If cladogenesis takes place by periph-
eral budding, with ancestral populations remaining intact and mostly
unchanged, then the actual phylogeny should be represented by ances-

calgariana   meadi

                              harmonia

              nevadensis   inornata

edwardsi   rupestris   macaria   comstocki

              semivirida   juba   callippe

                              elaine ——————— liliana
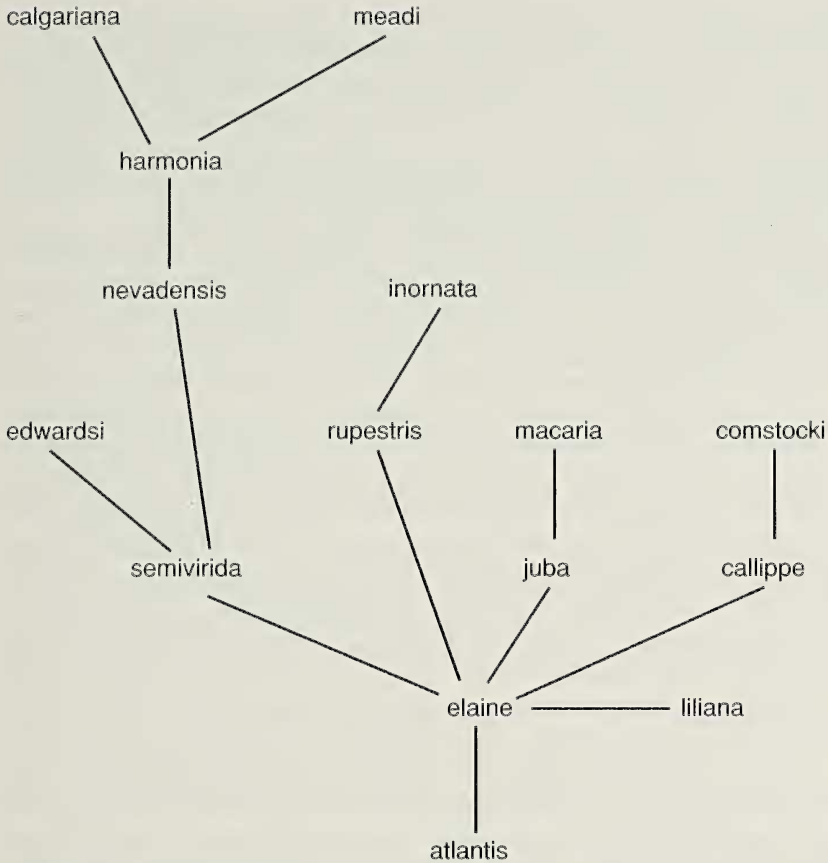
                              atlantis

Fig. 5.   Phylogenetic interpretation of *Speyeria callippe* subspecies.

tor-descendant relationships among extant taxa in the absence of extinc-
tions. Such an interpretation for the *S. callippe* group is presented in
Figure 5, and is based upon the cladistic data combined with the
distributions shown in Figures 2 and 4.

This family tree suggests that *S. callippe elaine* originated as a West
Coast isolate from *S. a. atlantis*, probably in western Oregon. Aside from
characters 1 and 2, *S. c. elaine* only differs from *S. a. atlantis* by a single
derived character (13), and this is a rather weak and inconsistent
character. Moreover, *S. c. elaine* still occupies a forest habitat like *S. a.
atlantis*, although it is a warm, dry forest of oak, pine, and fir. The
vicariance of *S. c. elaine* and the similar *S. c. liliana* is also suggestive of
considerable antiquity.

Other subspecies of *S. callippe* in California are more divergent, and
some races have shifted from the ancestral forest habitat to xeric
grasslands (*i.e. comstocki, macaria, inornata*). However, the most ex-
treme divergence shown in Figure 3 separates the *semivirida* group from
the *callippe* group. This change is closely correlated with an extreme

ecological shift, from the ancestral forest habitat to the semi-desert sagebrush steppes of the Great Basin and intermountain regions. Two of these taxa, *S. c. calgariana* and *S. edwardsi*, have moved east of the Rocky Mountains to occupy the xeric short-grass prairies of the northern Great Plains. In other words, the degree of morphological divergence is directly related to ecological divergence, from the cold, wet spruce forests of *S. a. atlantis* to the hot, dry grasslands of *S. c. calgariana*.

I believe that these examples provide at least indirect, circumstantial evidence in support of the theories of peripatric cladogenesis and punctuated equilibria. From the probable point of origin on the West Coast, *Speyeria callippe* populations have evolved and spread by the peripheral budding process southward and eastward across much of western North America. Lowland deserts and high mountain ranges combined with Pleistocene climatic fluctuations have likely served as isolating barriers during this process. Major morphological changes appear to be associated with the creation of new, descendant populations combined with major ecological shifts into new environments. At the same time, ancestral populations remain intact and locked into long-term stasis within their ancestral environments. Over long periods of time, ancestral types such as *S. c. elaine* may give rise to multiple descendants that differ greatly in age of divergence. For example, *S. c. juba* appears to be much older than *S. c. rupestris* by reason of its vicariance.

The above discussion does not mean that phyletic evolution never takes place within established gene pools. However, such change may be limited to simple genetic traits, rather than a major restructuring of the genome. Sperling (1987) has hypothesized that the black wing morph gene of *Papilio polyxenes asterius* has been introduced into sympatric populations of *P. bairdi* through hybridization, probably in New Mexico or eastern Arizona. The black gene has since spread throughout southwestern populations of *P. bairdi*, extending to southern California and southern Idaho. Such gene flow and phyletic evolution is most likely to take place in strongly vagile organisms with a cohesive population structure, and is much less likely in sedentary organisms such as *Speyeria* or *Euphydryas* species.

Literature Cited

ARNOLD, R.A. 1985. Geographic variation in natural populations of *Speyeria callippe* (Boisduval) (Lepidoptera: Nymphalidae). Pan-Pacific Entomologist 61:1-23.

BARTON, N. & G. M. HEWITT. 1983. Hybrid zones as barriers to gene flow. In: Protein polymorphism: adaptive and taxonomic significance. G.S. Oxford & D. Rollinson, eds. Academic Press, New York. pp. 341-359.

BOWDEN, S.R. 1979. Subspecific variation in butterflies: adaptation and dissected polymorphism in *Pieris* (*Artogeia*) (Pieridae). J. Lepid. Soc. 33:77-111.

BROWER, H.L. 1959. Speciation of butterflies of the *Papilio glaucus* group. I. Morphological relationships and hybridization. Evolution 13:40-63.

CARSON, H.L. 1982. Speciation as a major reorganization of polygenic balances. In: Mechanisms of speciation, C. Barigozzi, ed. Alan R. Liss, Inc. New York. pp. 411-433.

CARSON, H.L. & A.R. TEMPLETON. 1984. Genetic revolutions in relation to speciation phenomena: The founding of new populations. Ann. Rev. Ecol. Syst. 15:97-131.

CLARKE, C.A. & T.B. LARSEN. 1986. Speciation problems in the *Papilio machaon* group of butterflies (Lepidoptera: Papilionidae). Syst. Ent. 11:175-181.

COLLINS, M.M. 1984. Genetics and ecology of a hybrid zone in *Hyalophora* (Lepidoptera: Saturniidae). University of Calif. Pub. in Entomology 104:1-93.

CRACRAFT, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: Reconstructing the tempo and mode of evolution. Amer. Zool. 22:411-424.

DIMOCK, T.E. & R.H.T. MATTONI. 1986. Hidden genetic variation in *Agraulis vanillae incarnata* (Nymphalidae). J. Res. Lepid. 25:1-14.

DORNFELD, E.J. 1980. The butterflies of Oregon. Timber Press, Forest Grove, Oregon. 276 pp.

DOS PASSOS, C.F. & L.P. GREY. 1947. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. American Museum Novitates, No. 1370.

EHRLICH, P.R. 1961. Has the biological species concept outlived its usefulness. Syst. Zool. 10:167-176.

EHRLICH, P.R. & D.D. MURPHY. 1981. The population biology of checkerspot butterflies (*Euphydryas*). Biol. Zbl. 100: 613-629.

———. 1983. Butterflies and biospecies. J. Res. Lepid. 21:219-225.

EHRLICH, P.R. & P.H. RAVEN. 1969. Differentiation of populations. Science 165:1228-1232.

EHRLICH, P.R. & R.R. WHITE. 1980. Colorado checkerspot butterflies: isolation, neutrality, and the biospecies. Am. Nat. 115:328-341.

ELDREDGE, N. & J. CRACRAFT. 1980. Phylogenetic patterns and the evolutionary process. Columbia University Press, New York. 349 pp.

ELDREDGE, N. 1989. Macroevolutionary dynamics. McGraw-Hill Publishing Co. New York. 226 pp.

ENDLER, J.A. 1977. Geographic variation, speciation and clines. Princeton Univ. Press, Princeton, N.J. 246 pp.

EPLING, C. & W. CATLIN. 1950. The relation of taxonomic method to an explanation of organic evolution. Heredity 4:313-325.

ERWIN, T.L. 1981. Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In: Vicariance biogeography: a critique. G. Nelson & D.E. Rosen, eds. Columbia University Press, New York. pp. 159-183.

FERRIS, C.D. 1983. *Speyeria atlantis* phenotypes in the southern Rocky Mountains (Lepidoptera: Nymphalidae: Argynninae). J. Res. Lepid. 22:101-114.

FERRIS, C.D. 1987. A revision of the North American *Salix*-feeding *Colias* species (Pieridae: Coliadinae). Bull. Allyn Mus. No. 112.

———. 1988a. *Euphydryas anicia* and *E. chalcedona* in Idaho (Lepidoptera: Nymphalidae). J. Res. Lepid. 26:109-115.

———. 1988b. Revision of the North American Ericaciae-feeding *Colias* species (Pieridae: Coliadinae). Bull. Allyn Mus. No. 122.

FORD, E.B. 1945. Butterflies. Collins St. James Place, London. 368 pp.

FUTUYMA, D.J. 1979. Evolutionary biology. Sinauer Associates, Inc. Sunderland, Mass. 565 pp.

GILLHAM, N.W. 1956. Geographic variation and the subspecies concept in butterflies. Syst. Zool. 5:110-120.

GOULD, S.J. & N. ELDREDGE. 1977. Punctuated equilibria: The tempo and mode of evolution reconsidered. Paleobiology 3:115-151.

GOULD, S.J. & R.F. JOHNSTON. 1972. Geographic variation. Ann. Rev. Ecol. Syst. 3:457-498.

GREY, L.P. & A.H. MOECK. 1962. Notes on overlapping subspecies I. An example in *Speyeria zerene*. J. Lepid. Soc. 16:81-97.

GREY, L.P., A.H. MOECK, & W.H. EVANS. 1963. Notes on overlapping subspecies. II. Segregation in the *Speyeria atlantis* of the Black Hills. J. Lepid. Soc. 17:129-147.

HAMMOND, P.C. 1986. A rebuttal to the Arnold classification of *Speyeria callippe* (Nymphalidae) and defense of the subspecies concept. J. Res. Lepid. 24:197-208.

JOHNSON, G.B. 1976. Enzyme polymorphism and adaptation in alpine butterflies. Ann. Missouri Bot. Gard. 63:248-261.

LORKOVIC, Z. 1962. The genetics and reproductive isolating mechanisms of the *Pieris napi-bryoniae* group. J. Lepid. Soc. 16:5-19, 105-127.

MATTONI, R.H.T. 1989. The *Euphilotes battoides* complex: recognition of a species and description of a new subspecies (Lycaenidae). J. Res. Lepid. 27:173-185.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass. 797 pp.

——. 1976. Evolution and the diversity of life. Harvard University Press, Cambridge, Mass. 721 pp.

——. 1982. Processes of speciation in animals. In: Mechanisms of speciation, C. Barigozzi, ed. Alan R. Liss, Inc. New York. pp. 1-19.

McCORKLE, D.V. & P.C. HAMMOND. 1988. Biology of *Speyeria zerene hippolyta* (Nymphalidae) in a marine-modified environment. J. Lepid. Soc. 42:184-195.

MILLER, L.D. & F.M. BROWN. 1981. A catalogue checklist of the butterflies of America north of Mexico. The Lepidopterists' Society Memoir No. 2. 280 pp.

MOECK, A.H. 1957. Geographic variability in *Speyeria*. Milwaukee Entomol. Soc. Spec. Pap. 48 pp.

MURPHY, D.D. 1983. On the status of *Euphydryas editha baroni* with a range extension of *E. editha luestherae*. J. Res. Lepid. 21:194-198.

PIMENTEL. R.A. 1959. Mendelian infraspecific divergence levels and their analysis. Syst. Zool. 8:139-159.

PLATT, A.P. 1983. Evolution of North American admiral butterflies. Bull. Entomol. Soc. Am. 29:10-22.

REMINGTON, C.L. 1968. Suture zones of hybrid interaction between recently joined biotas. Evolutionary Biology 2:321-428.

RIGHTMIRE, G.P. 1985. The tempo of change in the evolution of mid-Pleistocene *Homo*. In: Ancestors: the hard evidence, E. Delson, ed. Alan R. Liss, Inc. New York. pp. 255-264.

RINDGE, F.H. 1987. *Speyeria* collection of Paul Grey to the American Museum of Natural History. J. Lepid. Soc. 41:123.

ROBINSON, R. 1971. Lepidoptera genetics. Pergamon Press, Oxford. 687 pp.

ROCKEY, S.J., J.H. HAINZE, & J.M. SCRIBER. 1987. A latitudinal and obligatory diapause response in three subspecies of the eastern tiger swallowtail *Papilio glaucus* (Lepidoptera: Papilionidae). Am. Midl. Nat. 118:162-168.

ROSEN, D.E. 1978. Vicariant patterns and historical explanations in biogeography. Syst. Zool. 27:159-188.

ROTHSCHILD, W. & K. JORDAN. 1906. A revision of the American Papilios. Novit. Zool. 13:411-752.

SCOTT, J.A. 1980. A survey of valvae of *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia*. J. Res. Lepid. 17:245-252.

———. 1988. *Speyeria atlantis* in Colorado: rearing studies concerning the relation between silvered and unsilvered forms. J. Lepid. Soc. 42:1-13.

SCRIBER, J.M. 1986. Origins of the regional feeding abilities in the tiger swallowtail butterfly: ecological monophagy and the *Papilio glaucus australis* subspecies in Florida. Oecologia 71:94-103.

SPERLING, F.A.H. 1987. Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). Quaest. Ent. 23:198-315.

STANLEY, S.M. 1979. Macroevolution: pattern and process. W.H. Freeman & Co., San Francisco. 332 pp.

STEBBINS, G.L. & F.J. AYALA. 1981. Is a new evolutionary synthesis necessary? Science 213:967-971.

THORPE, J.P. 1984. Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. Evolution 38:233-243.

WELLS, P.V. & J.D. STEWART. 1987. Cordilleran-boreal taiga and fauna on the central Great Plains of North America, 14,000-18,000 years ago. Am. Midl. Nat. 118:94-106.

WHITE, M.J.D. 1978. Modes of speciation. W.H. Freeman & Co., San Francisco. 455 pp.

WILSON, E.O. & W.L. BROWN, Jr. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2:97-111.

Table 1. Derived character state changes in the phylogeny of *Speyeria callippe* subspecies

1.   black median band at end of discal cell of dorsal hindwing distally elongate (versus not elongate)
2.   silver spot in discal cell of ventral hindwing (vhw) large (vs. small discal spot)
3.   yellow-orange ground color on dorsal wing (dw) (vs. medium orange)
4.   very heavy melanic basal suffusion on dw (vs. heavy suffusion)
5.   disc on vhw yellow-brown or pure yellow, red ground color on ventral forewing (vfw) reduced (vs. brown disc & heavy red color)
6.   median spots on vhw large and elongate (vs. short, pointed spots)
7.   small median spots on vhw (vs. larger spots)
8.   wide yellow submarginal band on vhw (vs. narrow band)
9.   disc on vhw yellow-brown or pure yellow (vs. brown disc)
10.   melanic basal suffusion on dw greatly reduced (vs. heavy suffusion)
11.   forewings rounded (vs. pointed forewings)
12.   reduced melanic basal suffusion on dw (vs. heavy suffusion)
13.   large and rounded median spots on vhw (vs. pointed spots)
14.   spots on vhw unsilvered (vs. silver spots)
15.   reduced melanic basal suffusion on dw (vs. heavy suffusion)
16.   ground color of vfw yellow in males (vs. orange color)
17.   veins in dorsal forewing of males thin with reduced dark scaling (vs. thick dark veins)
18.   yellow-orange ground color on dw (vs. medium orange)
19.   disc greenish brown on vhw (vs. brown disc)
20.   median spots on vhw large and elongate (vs. rounded spots)
21.   melanic basal suffusion on dw greatly reduced (vs. heavy suffusion)
22.   disc pure green without brown on vhw (vs. greenish brown disc)
23.   green suffusion over yellow submarginal band on vhw (vs. clear yellow band)
24.   disc gray or gray-green (vs. pure green disc)
25.   disc olive-green (vs. pure green disc)
26.   heavy melanic basal suffusion on dw (vs. little suffusion)
27.   large wind size (forewing length over 32 mm.) (vs. small wing size less than 32 mm.)
28.   long valve process on male genitalia (vs. short, club-shaped process)